Is Indeterminism the Source of the Statistical Character of Evolutionary Theory?*

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We argue that Brandon and Carson's (1996) "The Indeterministic Character of Evolutionary Theory" fails to identify any indeterminism that would require evolutionary theory to be a statistical or probabilistic theory. Specifically, we argue that (1) their demonstration of a mechanism by which quantum indeterminism might "percolate up" to the biological level is irrelevant; (2) their argument that natural selection is indeterministic because it is inextricably connected with drift fails to join the issue with determinism; and (3) their view that experimental methodology in botany *assumes* indeterminism is both false and incompatible with the commitment to discoverable causal mechanisms underlying biological processes. We remain convinced that the probabilism of the theory of evolution is epistemically, not ontologically, motivated.

1. Introduction. The question of why the theory of evolution is a statistical theory appears, like the poor, to be still with us. Rosenberg (1988, 1994) and Horan (1994) both argued that the theory's use of probabilities is a result of our epistemic limitations. Horan argued that if evolutionary processes are deterministic, then a statistical theory describing those processes might be useful, but is not necessary. Rosen-

berg argued that the theory will be statistical regardless of the deterministic or indeterministic character of evolutionary phenomena because agents with our cognitive limitations and our interests can only use the theory for explanations and predictions by imposing epistemic probabilities on them.

Brandon and Carson (1996) [hereafter BC] dispute at least one part of these analyses. They hold that the theory of evolution [hereafter ET] "is fundamentally indeterministic." More fully, they argue for a conditional:

> What we have shown is that *if* one is a realist in one's attitude towards science—that if one thinks that a primary aim of doing science is to develop theories that truly describe the mechanisms producing the phenomena, and if one takes theoretical fruitfulness and experimental confirmation as evidence for the reality of theoretical entities—*then* one should conclude that ET is fundamentally indeterministic. (336)

Actually we suspect that this statement of BC's misstates their position: that evolution (not, as they say here, evolutionary theory) is indeterministic, and that is why the theory is statistical. We shall therefore assume that their argument is that the theory is statistical because the phenomena are indeterministic.

We endorse the antecedent of this conditional, that the primary aim of science is to correctly describe the processes and phenomena in the domain of interest, but we reject the consequent. We reject the consequent—that we are obligated to conclude that evolution is fundamentally indeterministic—because we dispute their notion that the experimental confirmation and theoretical fruitfulness of evolutionary theory rests on an implicit commitment to indeterminism. We take up this interesting question in Section 5. Along the way, we reject three additional arguments BC provide in order to establish their conclusion that evolutionary processes are fundamentally indeterministic: their argument based on the popularity of the propensity interpretation of fitness (Section 2), their "percolation argument" (Section 3), and their drift argument (Section 4).

In the discussion to follow, it is important to be clear on the distinction between the theory of evolution and the process of evolution, on the one hand, and between probabilism and indeterminism, on the other. The theory is some kind of abstract object of inquiry, the process is what happens wherever the theory's laws, models, etc., are instantiated. Processes are indeterministic, theories are probabilistic or statistical. Indeterminism in a process is only one possible source for the probabilism in a theory. Even a statistical theory of an indeterministic

process may be statistical for reasons other than the indeterminism of the process. By contrast, most writers hold that quantum theory is probabilistic because quantum processes are indeterministic. Accordingly, we may describe quantum theory as (derivatively) indeterministic because the process it describes is indeterministic.[1] For present purposes, confusion will be minimized if we reserve "indeterminism" for the process, and "probabilistic" or "statistical" for the theory.

2. Indeterminism and the Propensity Interpretation of Fitness. BC begin by claiming that "the best and most influential treatments of the probabilistic nature of ET . . . (Beatty 1984; Sober 1984; Richardson and Burian 1992)" conclude that E is indeterministic (316).[2] As a claim about the "best and most influential treatments," this seems clearly mistaken,[3] although of course the issue is not decided by this appeal to authority. Nevertheless, they also find that the authorities have overwhelmingly weighed in in support of "the propensity interpretation of fitness (Brandon 1978, 1990; Brandon and Beatty 1984; Burian 1983; Mills and Beatty 1979; Richardson and Burian 1992) . . . which has been accepted by most philosophers of biology and many working evolutionary biologists" (ibid.), and they claim further that the propensity interpretation "presupposes that natural selection is fundamentally probabilistic" (ibid.).[4]

1. Some students of the subject, notably Nagel (1983), maintain that whether a theory is deterministic is a function of the state-descriptions it employs, and that under some state-descriptions quantum theory is deterministic after all. We will not explore this here, but this is an additional reason for caution in drawing conclusions about what we can determine about the objective chanciness of processes from whether or not the theories used to describe them use probabilities.

2. They actually write that these authors conclude that ET (the theory) is indeterministic, but we assume again that they mean to say that it is widely believed that evolution (the process) is indeterministic.

3. For instance, Sober (1984) argues that the theory of natural selection will be probabilistic even if Laplacian determinism is true: "Evolutionary theory is not committed on the question of whether determinism or indeterminism is true" (Sober forthcoming). This view suggests that any putative indeterminism of the processes is not the source of the theory's probabilism (unless one accepts an ad hoc disjunct to the effect that if the theory is statistical and the processes are indeterministic, then it is statistical because of the indeterminacy, but if the theory is statistical and the processes are determinate, then the statistics reflect something else). BC, in fact, and inconsistently, cite Sober to this effect a few pages away (336) from their (316) gloss that he is committed to the indeterminism of the processes under consideration.

4. When they say that writers presuppose that "natural selection is fundamentally probabilistic," we assume they mean that these writers presuppose that the process is indeterministic, not that the theory is probabilistic, inasmuch as there is no controversy over whether the theory uses probabilities.

Although Brandon's (1978) defense of the propensity interpretation of fitness does presuppose that natural selection is indeterministic, this strong ontological presupposition is not necessary. We might adopt a propensity view of fitness for epistemic reasons. If we knew about all the environmental forces impinging on organisms, we would find that fitness was perfectly correlated with reproductive success: two organisms with identical anatomical, physiological, and behavioral traits would have the same fitness value. But because we do not know what all these environmental forces are, we must describe the relation between an organism's traits and its potential reproductive success in probabilistic terms. Thus the probabilities used to measure expected number of offspring imply nothing whatever about any underlying indeterminism in the relationship that the organism bears to its environment—unless we assume at the outset that natural selection is indeterministic. The idea that these probabilities reflect our vast ignorance about all the dimensions along which we could measure the relationship of an organism to its environment (including stretching the environment over generational time, as Gillespie does[5]) is not called into question by the fact that we operationalize fitness using probabilistic measures.

Two recent criticisms suggest in any case that fitness cannot be appropriately operationalized by using probabilities to measure an organism's expected number of offspring in the ensuing generation: the propensity approach will sometimes err in assigning the same numerical fitness value to traits with different fitnesses. Beatty (1992), along with other objections, argues that the expected value approach cannot explain why it is that two traits with the same expected value but with different variances from the expected value differ in fitness. Sober (forthcoming) points to the same example, which is derived from the work of Gillespie (1973, 1974, 1977), to show why we must sometimes know more than what the expected value approach tells us in order to capture salient facts about fitness differences between two traits. When the same numerical measure of fitness (in this case the one calculated by the expected value approach) is assigned to two traits that differ in fitness, it is the approach that is at fault, not the notion that fitness is a deterministic effect of an organism's traits on its reproductive success in a particular environment.

3. Indeterminism and Percolation Effects. BC appeal to Bell's "no hidden variables" theorem in order to motivate the idea that quantum

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5. In repudiating the propensity interpretation of fitness, to which he had earlier subscribed, Beatty (Beatty and Finsen [neé Mills] 1989; Beatty 1992) has of course also urged that generational time is an important part of the fitness horizon of organisms.

indeterminism might manifest itself at the biological level. While they overstate the scope of the Bell results,[6] our contention here is even if quantum indeterminacy sometimes percolates to the level of biological processes, that would not be the source of the probabilities we find in evolutionary theory.

BC's treatment of how quantum indeterminism can " 'percolate up' in a powerful way to the level of populations [making] the evolutionary trajectory of such populations . . . genuinely indeterministic" (320) or "how quantum uncertainty . . . can have major evolutionary implications" (319) is only plausible because they mistakenly assume that a point mutation—i.e., a change in the nucleotide sequence of the DNA within a gene—will frequently shift a classically characterized dominant allele into its recessive partner or vice versa. They consider a population of two haploid genotypes, A and a, with relative frequencies p and q such that $p + q = 1$, the fitness of $A = 1 - q$, and the fitness of $a = 1 - p$. The gene frequencies have three equilibria: $p = 1$ (all As), $p = 0$ (all as), both of which are stable, and $p = .5$, which is unstable, because small perturbations from it would tend to result in selection driving the population to $p = 1$ or $p = 0$, given that the fitness of each allele depends precisely on its own frequency. They write, "Now suppose the population is at $p = .5$, and that a point mutation turns an A individual into an a. That population will go to $p = 0$. In another population at $p = .5$, a mutation turns an a into an A. That population goes to $p = 1$, and so on" (319). The upshot of this story is that (1) *if* indeterministic quantum events caused the point mutation,[7]

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6. BC write that Bell's theorem rules out *all* so-called "hidden variable" deterministic quantum theories (316, 317, 318). But the Bell correlations at most exclude *locally* deterministic theories (as they inconsistently recognize on 318). And despite BC's claim that the parsimonious physicist opts for locality over determinism, parsimony does not in fact come into the question. Physicists who reject local hidden variables do so because of the weight of the evidence from relativity theory that locality obtains. Furthermore, contrary to what BC claim on p. 336, there is no "*logical* inconsistency" (our emphasis) in positing hidden variables to account for the Bell correlations. Rather, the Bell results indicate that if there were such hidden variables, they would be non-local or even, as Huw Price (1996), Phil Dowe (1996) and others have proposed recently, it may be that the Bell correlations are a function of hidden variables operating backward.

7. Of course, saying that point mutations are caused by quantum activity is not the same thing as saying that point mutations instantiate quantum indeterminacy. Consider the shape and complexity of an adenosine molecule. The changes required to mutate this molecule into a guanine molecule would be quite considerable, clearly involving a substantial aggregation of micro-processes. Because the outcome of micro-events aggregating to this extent is asymptotically deterministic at even the level of macro-physical processes, BC's assertion that the processes creating point mutations are indeterministic is an assumption very much in need of a defense.

(2) *if* the point mutation occurred in an (a) haploid population where (b) the fitnesses of the competing alleles are dependent on nothing other than their own frequencies, (3) *if* the point mutation succeeds in changing the dominant allele into the recessive allele or vice versa, and (4) *if* one of the alleles then went to fixation, which would be a macro-event, *then* a quantum event has percolated up to the macrolevel and the equilibrium that results is at least partly a function of quantum indeterminism.

This is a story with a vanishingly small chance of occurring, and not just because all of the antecedents need to obtain. It requires that a single point mutation, one changing a cytosine into a uracil, for example, will result in the nuclear material which codes for the product of the *A* allele now switching to code for the product of the *a* allele. Given the size of even the smallest genes, the redundancy in the code, and the relatively small effect of amino acid substitutions in homologous proteins, the odds of this step alone occurring are overwhelmingly improbable (or, as we are tempted to say here, the odds asymptotically approach zero). Furthermore, this BC thought experiment is conceptually problematic from their point of view, in that it works only by treating the processes involved, except one point mutation, as deterministic. The hypothesized selective pressures on the alleles are treated as hegemonic and the outcome of those selective pressures as certain, while the possibility of additional 'random' events occurring to offset the point mutation is overlooked. This means that what is already an extraordinarily minute chance that a quantum indeterministic event has ever percolated up to the level of a biological process is predicated on premises that BC themselves regard as false.

As Rosenberg (1994, 61) and Horan (1994, 83, fn. 1) have already noted, it is not in principle impossible that quantum indeterminacy might occasionally alter a biological outcome. But the question is: Is this *why* we have statistical theories in evolutionary biology? Consider macrolevel physics, which successfully treats the objects and processes in its domain as if they were deterministic. Macrolevel physical processes and objects asymptotically approach determinism, in spite of whatever quantum percolation events may occur between the micro- and macro- levels. No reason has been given to suppose that quantum indeterminism hooks up to biological processes in some way that is quite different from how it hooks up to macrolevel physical processes. This leads us to suppose that biological processes, although they may be subject to some quantum indeterminacy, should also asymptotically approach determinism and should thus be describable, as macrolevel physical processes are, with a nonprobabilistic theory. However, since biological processes are *not* so described, and since this is not, per the

foregoing, a function of objective quantum chanciness, we infer that the statistical character of evolutionary theory is a reflection of our epistemic limitations and interests.

4. Bottlenecks and Whole Numbers: If Drift is Inevitable, Does Indeterminism Obtain? It is somewhat standard to write that evolution has occurred whenever the frequency of a gene, or a genotype, changes from one generation to the next. Gene frequency changes in a population can come about through a number of different agencies, obviously including natural selection and drift. But if we define evolution as any change in gene frequency, a further question arises as to whether some cases of gene frequency changes really should count as 'evolution'. Sewall Wright, while he agreed with Motoo Kimura that drift was causing nucleotide replacements to "[occur] at a very high rate" (Wright 1967), was less clear that these changes of molecular genetic constitution should count as cases of evolution: "With regard to the evolutionary importance of sampling drift, there is the dilemma that the condition that gives the maximum amount of such drift is that of complete neutrality and hence of no evolutionary significance" (ibid.).[8]

These concerns notwithstanding, BC adopt as their definition of drift "any transgenerational (evolutionary) change in gene or genotype frequencies due to sampling error" (321). In statistics, sampling error refers to the deviation of the value of a sample statistic from the value of the parameter describing the population from which the sample is drawn. Assuming that no other evolutionary forces are operating, the smaller the sample taken from the parental population the higher the probability that allelic frequencies in the offspring generation will move away from parental frequencies. Since samples are never infinite, there is a non-zero probability that allelic frequencies will so move. Some philosophers (e.g., Hull 1974, Beatty 1984) hold that the theory of evolution is statistical precisely because of this fact. If we accept this view, the following question remains: Are the probabilities employed in the theory epistemic or not?

Horan and Rosenberg both argue that the probabilities in question

8. The distinction that Wright makes, between evolution defined as gene frequency change *simpliciter* and evolutionary changes that are actually significant bears further investigation. In apostrophizing "Darwinian fundamentalists", Stephen Jay Gould says that evolutionists who emphasize the centrality of selective forces in evolution are quite behind the times because "Population genetics has worked out in theory, and validated in practice, an elegant, mathematical account of the large role that neutral, and therefore nonadaptive, changes play in the evolution of nucleotides" (1997, 35). This comment appears to be unalive to Wright's point.

are epistemic because sampling that results in a transgenerational drift of allelic frequencies reflects the operation of factors, including genetic drift, mutation, migration, and the forces governing chromosomal segregation, about which we have inadequate information. These factors are captured for the theory in epistemic probabilities. What this means is that if all this information were available to us, and we had the computational abilities needed to process it, the theory would not rely on probabilities. The two arguments that BC provide in order to show that evolutionary processes are indeterministic (and hence, in their view, *must* be described using a statistical theory) actually argue for a different thesis: that drift is inevitable. However, it is only when one already assumes that the use of evolutionary probabilities is motivated by ontological constraints rather than by epistemic ones that the indeterminism of evolutionary processes follows from "the inevitability of drift." Thus, as will emerge in our discussion of their two examples relating to drift, they have failed to join the real argument.

According to BC, drift is not just the probable outcome of certain biological sampling processes such as reproduction, it is sometimes *necessary*. "We have shown, for the first time as far as we are aware, that certain situations . . . which are easy to produce experimentally, and which must occur at least sometimes in nature . . . *force* drift to occur as opposed to merely making it more probable" (322–323). The picture they have in mind in their first example of forced drift is illustrated by the following hypothetical example. Suppose there is an allele A with a frequency of .01 in generation 1 of a population of 1000 which falls to 10 in generation 2 "due to a crash in environmental resources, a sudden explosion of predators, or experimental intervention" (322). With only 10 organisms left in generation 2, the frequency of A has gone to $> .1$ or has gone to 0. There is no third possibility (i.e., there is no possibility that the frequency of A in generation 2 is .01). Consequently, in this scenario drift must occur.

The three proposed reasons BC give to account for the population bottleneck that results in an intergenerational change of gene frequency are usually recognized as cases of natural selection. It is quite possible, for example, that the ten organisms in generation 2 got there because their parents were relatively better at evading predators, or at locating scarce resources, or had the characteristics that experimenters were looking for. Indeed, if we make the example into a genuine case of drift, by stipulating that the survival of the original ten members of generation 1 was not related to any superior fitness that they enjoyed over their conspecifics, including any fitness differentials that may have arisen from either possessing or not possessing rare allele A, then this is an episode of drift by definition, not by example. Even so, this ex-

ample has no implications for our thesis that evolutionary probabilities reflect epistemic limitations. The question from the point of view of the determinist/indeterminist dispute is not whether the gene frequency will change from generation 1 to generation 2. It is whether we would be able to predict that gene frequency change if we had enough information. There is nothing at all in this story to suggest that an omniscient being would not be able to determine, in advance of the fact, the frequency of gene A in generation 2; rather, BC are simply presupposing the reality of biological indeterminism.

It is not without interest to consider the experimental ramifications of BC's claim that in these circumstances, drift is forced to occur, as opposed to merely being more probable. The distinction between a probability of 1 and a merely high probability has not been salient from an experimental standpoint, and it is not clear how it could be made salient. When Theodosious Dobzhansky roamed the canyons of Death Valley and Mt. San Jacinto looking for small and isolated populations of *Drosophila pseudoobscura,* he hoped to find experimental evidence that would support Wright's view of evolutionary processes and undermine R.A. Fisher's opposing view. Wright's theory, at that time, was that nonadaptive differentiation between species occurred as a result of drift in small, isolated populations. Dobzhansky hoped to establish that small, isolated populations occurred in nature, and to measure the size of those populations by comparing the retention rate of recessive lethal alleles to the rate at which they occurred via mutation. If the retention rate was lower than the rate at which these lethals arose in the population, that suggested that the retention rate was being reduced because the alleles existed in populations where a relatively high degree of inbreeding occurred. Since a relatively high rate of inbreeding would most likely occur in small, reproductively isolated populations, low retention of recessive lethals would experimentally establish, Dobzhansky thought, that such small, isolated populations did exist in nature. If so, there would be an extremely high probability (but not a probability of 1) that drift would occur. Fisher did not doubt that we could assume, for all intents and purposes, that drift was occurring in situations like this. So, the issue was not whether drift was occurring with a high probability versus whether it was occurring with a probability of 1. Rather, for Fisher, the question was whether any of this drift led to evolutionarily significant outcomes along, of course, with his concern that we might fail to note selective forces operating on the alleles in question.[9]

9. Dobzhansky did not carry through this experiment, because Wright pointed out to him that the equations used to determine the mutation rate at which rare lethals ap-

We now turn to BC's second example of the ineliminability of drift, which is more ambitious than the first in that it purports to show not only that drift must occur occasionally, but that natural selection *itself* is "*indeterministic at the population level because (in real life as opposed to certain formal models) it is inextricably connected with drift*" (324, italics in original). Since BC have not actually shown that the probabilistic predictions and explanations employing drift are a function of indeterminism rather than forced upon us by epistemic limitations in a deterministic world, we of course do not agree that the mere condition of being "inextricably connected with drift" would force us to be indeterminists about natural selection. Nevertheless, it is worthwhile to consider the details of the example.

BC's argument models parent/gamete sampling with the classic example of balls drawn from an urn. Instead of red and black, here half the balls are sticky and the other half are slippery. There are 10,000 balls, and sticky balls have twice the probability of being drawn as slippery ones; their relative fitness is thus 1 and the slippery balls' relative fitness is .5. If ten balls are drawn, the (mathematically) 'expected' number of sticky balls drawn is $6\frac{2}{3}$. Mathematical expectation here is a technical term, meant to represent the *average* number of sticky balls that would be drawn if the process occurred an infinite number of times in identical circumstances. But of course, the mathematical expectation that $6\frac{2}{3}$ sticky balls and $3\frac{1}{3}$ smooth balls will be drawn will never actually occur since only whole balls can be drawn. If six sticky balls and four slippery ones are drawn the deviation from the mathematical expectation is alleged to be a case of drift. The conclusion drawn by BC is that since all real populations are finite, whenever probabilities of being sampled from generation to generation are neither 1 nor 0, "at the population level natural selection is indeterministic because with finite populations selection does not eliminate the drift-effects of sampling error . . . selection in finite populations always involves the possibility of drift . . . and as our numerical example shows, some situations *force* drift to occur" (325).

In a moment, we show how this argument simply presupposes the reality of biological indeterminism. But there are other reasons to reject it which we canvass first.

Consider the following odd consequence of their model. Although BC claim that "the smaller the sample size the more likely drift [where

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peared were based on "an infinitely large, random breeding population" (1938). This assumption appeared to Wright to be both (1) ineliminable and (2) undermined by the purported conclusion of the experiment, so that any results based on using this mutation assumption would be conceptually incompatible with the desired outcome.

they mean drift as in the difference between the mathematical expectation and the real result] is to occur" (325) and although this *is* true of real, biological drift, it is not true of their example. If I draw 10 balls, the mathematical expectation is that I will draw $6\frac{2}{3}$ sticky, $3\frac{1}{3}$ smooth. If I draw 1000, the mathematical expectation would be $666\frac{2}{3}$ sticky, $333\frac{1}{3}$ smooth. The minimum difference between the mathematical expectation and any actual result would still be at least $\frac{1}{3}$. This *absolute* difference, which is the basis of any plausibility their example might initially have, will never decline, no matter how high the number of draws. So, there is no connection between the size of the population, such that drift would *decrease* with increasing population size, and this absolute differential upon which BC's claim rests. Indeed, the only factor that influences whether the real result conforms to the mathematical expectations in their scenario is whether the exact number of draws just happens to be a smooth multiple of whatever the selective coefficients are.

If this argument establishes the indeterminism of the underlying processes, then so does the following parallel argument. Consider a world that is claimed to be deterministic. Take a fair coin, that is, one with a probability of landing heads of .5. Toss the coin once and destroy it. The result will have deviated from the mathematical expectation. Therefore, determinism is false. We take this to be a *reductio* of their argument.

Even if drift were evidence for some genuine indeterminism and even if natural selection inevitably co-occurred with drift, that is no reason to assert, as BC do, that this means that natural selection *itself* is indeterministic. Theories can be statistical because some phenomena in their domain are indeterministic, while other phenomena in the domain are deterministic. So even if we had a statistical biological theory, and we knew that some events in the domain of the theory were objectively chancy, and we knew that the theory was statistical because of those indeterminacies, this does not go any distance to establishing that all the phenomena in the domain of the theory are indeterministic. There are "mixed" theories like this in physics, where some of the phenomena involved are known to be indeterministic and some are presumed to be deterministic. The fact that deterministic and indeterministic processes may co-occur in a domain of interest does not mean that all the theories of that domain must be statistical.

The foregoing notwithstanding, our primary objection to BC's argument is that it *presupposes* objective chanciness. BC write: "[This] example is one where, by hypothesis, we know all there is to know about the situation yet drift can occur, and sometimes must occur, along with selection" (325). But of course, it is precisely not true that

we know all there is to know about this situation. The point of our thesis that evolutionary probabilities reflect epistemic limitations is that an omniscient being would not be using probabilities at all to guess at outcomes in situations like this. Rather, she would know, for each draw from the urn, whether a sticky ball or a smooth ball would be drawn, and would not be left staring off vaguely into the middle distance wondering why she drew 7 sticky balls when her prediction was that she would draw 6⅔. What our omniscient being would know about gene frequency changes from one generation to the next is parallel: she would simply know the fate, and the reasons for the fate, of each gene in generation 1 as it either moved, or failed to move, into generation 2.

5. Who Bears the Burden of Proof: Determinists or Indeterminists? BC rightly recognize that in order to infer from this case that natural selection is in fact indeterministic, we need to exclude the operation of so-called "hidden variables," factors that deterministically influence the drawing of each ball actually sampled. It is here that they finally join the issue with determinism, and they attempt to show that there is "no scientifically justifiable reason to suppose there are such hidden variables" (327).

This time their argument is not based on a model, but on the citation of an experiment performed by a botanist who cloned individuals from three different grass species and grew the cloned individuals in different soils. BC want to infer indeterminism from the variation in inflorescence mass, total plant biomass, and root-to-shoot ratio that appeared among the clones even though they were planted in "carefully controlled identical soil preparations on the same tabletop in the same greenhouse at the same time" (329). But to infer from such experiments the violation of the principle of same cause, same effect—i.e., indeterminacy in the chain from germination to completed development—we need to establish that conditions were in fact identical.

Now everything we know about the molecular biology of the gene and development tells us that conditions are not identical among clones, nor for that matter among clones-in-their-environments. To begin with, genetic replication does not proceed perfectly, and some nucleic acid substitution "mistakes" go undetected. A tiny quantity of such mistakes will make for phenotypic differences. Indeed, the number of them is so small as to make BC's "percolation" argument moot. But it is worth noting, again, the BC cannot have it both ways—denying the effects of nucleotide substitution in this case while attempting to exploit these alleged effects in their "percolation" argument. A more important source of deterministic differences is to be found in "developmental noise." This is a well-known phenomenon that by itself pro-

vides ample occasion for variation among clones as they grow, and does so without recourse to indeterminism. The experiments BC report did not control for the identities, similarities and differences of individual molecules either in the clones or in the soils contiguous to them. No experiment could control for these variables. But by themselves these factors are enough to produce variation along all the dimensions BC mention. In fact it is just because there are no truly identical clones, and no qualitatively identical experimental conditions in biological (even in molecular biological) experiments that biologists produce multiple clones and subject them to experiments. Otherwise, one genotoken in one pot would suffice.

Above we wrote that developmental noise would lead to differences in grass blade length "without recourse to indeterminism," holding that the default position here is determinism, and the burden of proof is on the shoulders of those who hold that the variation among cloned grasses results from indeterminism. Indeed, the burden of proof is on the indeterminist against the much weaker position that not *all* of the variation between clones is due to chance. That this should be the default position in the absence of evidence follows from the fact that all of chemistry, organic chemistry, molecular biology, and cellular physiology that one would invoke to explain the actual character of each blade of grass is deterministic (with the possible exception of second law considerations from thermodynamics, which are of doubtful relevance here). Even quantum mechanics recognizes that at the level of the macromolecule, nature asymptotically approaches determinism.

Of course if the variation among clones is the result of quantum mechanical indeterminacy in the action of individual molecules, atoms and other microparticles in the biosynthetic pathways from the nucleic acids to the developed grass blade, then the resulting variation will be a case of indeterminacy. According to BC, the burden of proof here rests with those who hold that the variation in grass blade characteristics is the result of deterministic hidden variables. But they argue for this distribution of the burden of proof from a false premise:

> It is beyond doubt that the positing of genuinely probabilistic propensities governing the evolutionary fates of individual organisms has been an integral part of the impressive development of evolutionary population genetic theories in this century . . . all the available empirical evidence supports this idea. In contrast, the positing of deterministic hidden variables in evolutionary theory serves no theoretical purpose at all, and, insofar as it is allowed to be addressed by data is contradicted by empirical data. (331)

We see the matter quite differently. First, it seems to us that population genetics, impressive or not, has not taken sides on whether the probabilities it employs are epistemic, grounded or ungrounded probabilistic propensities, or long run relative frequencies. Despite the sincerity of their assertion, it is tendentious to attribute the advances of population biology to the *interpretation* of its probabilities rather than to its *use* of probabilities (no matter how interpreted), or to some other feature of the theory, say its reliance on adaptationism or the assumptions of particulate inheritance and sexual reproduction. Second, however one interprets the probabilities of ET, they do not have the same "credentials" which make the probabilities of quantum mechanics attractively viewed as propensities. What the available evidence suggests is that at the level of the macromolecule and above, biological processes asymptotically approach determinism, and this should be the working assumption. Third, the "positing" of deterministic hidden variables in evolutionary theory has been essential to such theoretical advance as it has shown. The discipline has advanced by seeking out causes for persistent and unexpected outcomes. For example, adaptationism is nothing more than the assumption that there are selective causes for features even when these causes are not obvious or are not apparent to us.

BC ask rhetorically, "why posit hidden differences among the flower pots? . . . The indeterminist accounts for them by positing probabilistic propensities governing the behavior of the plant" (333). Well, then, the indeterminist is no biologist. For a biologist, even one who would appeal to probabilistic fitness propensities, faced with variation of the sort in question, and seeking to explain it, will not do so by appeal to such propensities. He or she will "posit" hidden variables and seek evidence for them in more carefully constructed experiments. To do otherwise is to abdicate the scientist's self-appointed tasks.[10]

In this connection, it is worth comparing evolutionary probabilistic

10. In effect, the experimental biologist's research program proceeds on something like the thesis of "mereological determinism" which BC attribute to Rosenberg (328–329) and stigmatize as either analytic and untestable or synthetic and false. The principle holds roughly that for all times t, the micro-state of a system at t determines the macro-state of the system at t, and determines the micro-states of the system at $t' > 1$. This statement they claim to be refuted by Stern-Gerlach experiments. Of course it is refuted by far more well-known phenomena: radioactive decay, for example. But the principle's methodological relevance remains in force where nature asymptotically approaches determinism. And it is clear that in Rosenberg (1984, 1994) the micro-states in question are taken to be macromolecular ones (and indeed relations between macromolecules and their environments), and not quantum mechanical ones. BC's appeal to Stern-Gerlach is thus irrelevant to their argument against mereological determinism as a methodological rule in biology.

propensities with quantum mechanical ones. BC note rightly that "the positing of theoretical entities is taken seriously when (1) the positing of the entity aids the development of the theory; and (2) the available empirical evidence supports the posit" (331). These two principles help explain why pure probabilistic propensities are viewed as an uncomfortable but unavoidable conclusion in quantum mechanics. They are indeed a posit in physics, and a reluctant one. Evolutionary theory has no need of such posits, not yet, perhaps never.

In brief, the probabilities of quantum mechanics are treated as dispositions ungrounded by further manifest or occurrent properties (hidden variables, for instance) because no other interpretation of them seems tenable. The interpretation of the absolute value of the square of the Psi-function as an epistemic probability, in accordance with a Copenhagen approach to quantum mechanics, is problematical because it is overtly idealistic. Interpretations of quantum probabilities as long run relative frequencies face all the problems of the relative frequency approach and do not have uncontroversial implications for any finite actual frequencies. Therefore, despite the absence of any independent empirical evidence for manifest properties of quantum preparations to ground pure probabilistic propensities, many physicists and philosophers have embraced them *faut de mieux*.

In fact, BC even identify the methodological commitments of physics which makes the postulation of probabilistic propensities in quantum mechanics uncomfortable, and their postulation in evolutionary biology intolerable. They endorse the thesis that it is a "primary aim of doing science . . . to develop theories that describe the mechanisms producing the phenomena" (336). Ungrounded probabilistic propensities are not mechanisms; they are admissions that there is no mechanism operating to give rise to actual distributions of dependent variables and observed correlations.

It is because evolutionary theory is committed to the existence of such mechanisms that it can have no truck with such probabilities or the indeterminism they engender. Unlike quantum mechanics, evolutionary biology is not a science at the basement level, and its variables are realized presumably by complex combinations of more fundamental variables. To posit the existence of ungrounded dispositions, i.e., pure probabilistic propensities, in evolutionary theory does not aid in the development of the theory, and the evidence across the sciences weighs against this posit. Of course this evidence does not tell against the employment of probabilities *per se* in evolutionary theory, just against ungrounded dispositions of organisms and populations, as opposed to, say, epistemic probabilities. In consequence, BC's argument to "the scientific absurdity of the determinists' position" is moot.

6. Conclusion. It is not the case that hidden variables are posited "for no reason other than to save the deterministic character of [evolutionary] theory" (BC, 333). Rather, they are posited in order to be discovered. Advances in evolutionary theory consist in large part in discovering these variables. What would be absurd is to suppose that the statistical character of evolutionary theory reflects ungrounded propensities of populations, causally inexplicable by the manifest properties of organisms on which they supervene.[11] Such propensities are hard enough to swallow in physics. In biology they are completely superfluous.[12]

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11. Absurd or not, BC may have made this mistake as well. They criticize Horan's (1994) claim that if fitness supervenes on phenotypes, then the relationship between phenotypes and fitness is deterministic. BC write that her assertion "seems to beg the question against the proponents of the propensity interpretation of fitness who think (a) fitness is a supervenient property; and (b) it is a probabilistic, not deterministic, dispositional property" (327). Denying that the supervenience of a macro-state (like fitness) requires its mereological determination by the microproperties on which it supervenes, as BC seem to do, simply abdicates the scientist's responsibility to seek the underlying factors that give rise to a supervenient property. Similarly, Millstein's (1996, S17) claim that an omniscient being would "miss the population level explanations" that statistical theories provide—if not simply false or tautologous—appears to ignore the fact that (descriptive) statistical properties supervene on the properties of individuals belonging to the populations the statistical properties describe. Cf. Footnote 10 above and Horan forthcoming a and forthcoming b.

12. We pass over BC's last argument, one that claims that because the probabilistic generalizations in ET are explanatory, the probabilities they quantify over must be objective and not epistemic. This is a non sequitur. Evolutionary probabilities are indeed potentially explanatory. But nothing follows directly from this about their reality unless we adopt certain controversial accounts of explanation. For that matter, on at least some accounts of explanation, epistemic probabilities will be perfectly explanatory as well. Consequently, the role of probabilities in explanation decides nothing in regards to varying interpretations of probability or any dispute between determinism and indeterminism, inside biology or outside of it.

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